

Courtship Activities in the Red-throated Diver (*Colymbus stellatus* Pontopp.); together with a discussion of the Evolution of Courtship in Birds*. By JULIAN S. HUXLEY, M.A. (Communicated by Prof. E. S. GOODRICH, M.A., F.R.S., Sec.L.S.)

(PLATES 14, 15, and 4 Text-figures.)

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THE following paper is a continuation of previous work on the sexual relationships in species of birds in which both sexes possess bright colours and also exhibit similar sexual ceremonies. The reader is referred to papers on the Great Crested Grebe and on the Dabchick (Huxley, '14 and '19). It is unnecessary to recapitulate at any length, but certain general conclusions may be stated.

1. In most, possibly all monogamous birds, a pre-mating and post-mating period may be distinguished. "Courtship" activities usually occur during both of these periods; but the majority of the "courtship" actions which are to be found described in the literature occur in the post-mating period, and therefore cannot be operative in any true form of sexual selection as imagined by Darwin. So far as pre-mating ceremonies occur and are effective in the choice of mates, they can of course find place in a scheme of true sexual selection.

2. In birds in which the sexes are quite or almost similar, and both adorned with bright colours or special plumes, or other structures, which are displayed or otherwise used in sexual ceremonies, both sexes play a quite or nearly similar rôle during "courtship"; very often ceremonies occur in which both sexes simultaneously play a similar rôle; for such ceremonies the term "mutual" is employed.

3. These mutual ceremonies may be "self-exhausting"—that is, may end in the birds resuming the ordinary routine of life; or they may be a means of raising the emotional tone as a direct or indirect excitant to coition. In the Grebe, where self-exhausting display ceremonies were the rule, special pre-coition ceremonies were found, in which attitudes resembling those employed at coition were adopted.

4. An association of various of the birds' other activities with the sexual ceremonies was often observed. The "handling" of nest-material is frequently so associated, as has been noted by many previous observers; but actions like those of preening or of shaking the head, although originally quite without sexual significance, may also be used as part of the raw material of sexual ceremonies.

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5. In many birds similar in the two sexes both male and female incubate. In many but not all such species the relieving of one bird by the other on the nest is the occasion for a special sexual ceremony, which in its turn may or may not be used at other times. This ceremony of nest-relief appears to be absent in the Grebe.

With this brief introduction, we may pass to the observations on the Red-throated Diver. These were made while the writer was on the Oxford University Expedition to Spitsbergen, 1921. Most were made on Prince Charles Foreland, an island 60 miles long, off the west coast, on which a small party of us camped for 11 days, from June 30 to July 10. Numerous small freshwater pools are found here, as in many other places near the coast in Spitsbergen; and on a great many of these, at any rate on the north-western and western coasts, Divers are to be found nesting. We were fortunate in being encamped on the shores of Richard Lagoon, a sheet of brackish water about a mile wide and 5 miles long, communicating with the sea by one narrow opening. This lagoon was the scene of much of the Divers' courtship, both pre- and post-mating, though especially the former. Much of the birds' feeding was done on the open sea; but for rest and courtship the lagoon was chosen. Even after incubation had begun, the birds appeared to come down to the lagoon when not sitting; it was the scene of veritable social gatherings of Divers, four or five being commonly on its waters together, and eight having been seen there on one occasion. Sometimes they would fish, progressing by means of long dives, as does the Crested Grebe; at other times they would stay quiet, resting or preening themselves. But during the period of our stay we never observed two or more Divers on the lagoon without some courtship action following within a comparatively short time. The male and female are similar in appearance; the female is smaller than the male, although the wing and beak measurements of species overlap somewhat. However, the female appears to have a much less massive neck than the male, and a separation of the sexes can usually be made with reasonable probability.

Description of Chief Courtship Actions.

It will be best to begin with a description of the chief types of actions seen, following this with their probable interpretation.

1. "Plesiosaur race." This ceremony was so christened because the attitude adopted by the birds in its performance made them resemble miniature Plesiosaurs half out of water (fig. 1). Usually two or three birds took part in it, sometimes four. The birds depressed the hinder half of the body below the water; the body was held at an angle so that the breast and shoulders were stuck out; the neck was stuck upwards and forwards in a stiff position, the head and beak inclined somewhat forward, again somewhat stiffly. In this attitude the birds swam through the water, accompanying one another.

Their passage through the water seemed to be accompanied by a good deal of resistance, since a wave showed at their breasts. They would go for some distance in this way; then would often turn and continue the process in the opposite direction. The bird which had led in one direction, it seemed, might be replaced by another as leader after turning. The whole ceremony did not give the idea of a true pursuit, such as is seen among many birds, but more of a race, or of something still more ceremonial and formal.

The most usual arrangement is for one bird to lead, the other one or two being half a length or less behind. Various modifications of the pose are seen. Sometimes the body is at a very low angle, the neck little arched, the head and bill almost horizontal; at others the tail is more submerged, the breast more elevated, the neck much arched, and the head and bill pointed downwards; it is in this pose that the likeness to a Plesiosaur is most marked. Occasionally almost the whole of the body is submerged. As to the general appearance, I quote from my notes:—"There is a strange stream-line effect about the creatures. They must be paddling with great energy to keep up

FIG. 1.



Red-throated Diver: Plesiosaurus-race ceremony.

the speed." "There is often a snaky look about them when in the semi-vertical attitude." Altogether the effect as of tension, of emotional ritual, so familiar to all those who have watched birds during courtship, is marked.

A still further modification of the pose is sometimes seen in what may be called the "wing Plesiosaur attitude." In this the wings are stretched out nearly at right angles to the body, perhaps $2/3$ spread, the point inclined a little backwards, and somewhat drooped, so that the upper surface is plainly visible. This might be adopted by all the birds in a "race," or by the "pursuer" alone in a "race" of two birds only. The same attitudes and relative positions were maintained by one such pair of birds for over 50 yards.

Occasionally birds might be seen in a still more nearly vertical attitude. When this was so they did not progress fast.

A peculiar note invariably accompanied this ceremony. I find it described in my notes as "a growl with a bubble in it" or a "rolling growl." This is repeated a number of times, and appears to be used just before or at the beginning of the ceremony proper. This note did not seem to be used at any other time, except in the "snake-ceremony" (see p. 257).

From the beginning we noticed that birds engaged in this and in other sexual ceremonies, or more often when under the influence of sexual excitement, but not actually engaged in a ceremony, often engaged in curious and apparently meaningless actions. The most frequent was the dipping of the beak in the water (fig. 2), often repeated several times within a few minutes; a variation of this consisted in "looking into the water"—in other words, the submerging of the beak and fore-part of the head for some little time; finally, shaking of the head was observed, though much more rarely than in the Grebe.

FIG 2.



Red-throated Diver: snake-ceremony.

It became quite certain, as we continued our observations, that these actions, or at least the two former, were definitely associated with sexual excitement. Like the head-shaking and "habit-preening" of the Grebe (Huxley, '15), they appear to represent actions normally performed with some other function, or, if functionless, with non-sexual associations, which have become, through some peculiarity of the psychological mechanism, secondarily associated with sexual excitement, and used as physical expression of sexual emotion. This appears also to be the case with a special form of dive which I call the "splash-dive." In this, instead of submerging quietly, almost

FIG. 3.



Red-throated Diver: emergence ceremony.

without a ripple, as is done when the birds are diving for food or to escape danger, the bird gives a sharp kick with the legs as it goes under, sending a shower of spray into the air; furthermore, the dive is for a very short distance, the bird emerging generally about 5 or 6 yards away. This, too, is associated with apparently all forms of sexual excitement, and otherwise is used only under the influence of the emotion of anger (see Van Oordt and Huxley, '22). Here we have apparently a normal form of activity, which is used in a modified form when associated with sexual emotion.

2. A very remarkable ceremony, unfortunately only observed clearly on one or two occasions, was the dive followed by vertical emergence (figs. 3 & 4). In the best-observed case two birds out of a party of three were close together. Suddenly one—almost certainly a female—dived (with a splash). The other—almost certainly a male—immediately spread its wings and half flew, half sputtered along the surface of the water for 5 or 6 yards. The bird which had dived then came up out of the water close to the other, in an almost vertical position (fig. 3). The neck was held so as to continue the line of the body; the head bent down so that the bill made a small angle with the breast. The emergence was fairly slow. It stayed in this position for perhaps 5 seconds, then settled down on the water. Here we have a ceremony which is extremely similar to one which I have described in the Crested Grebe, although not quite so elaborate. Its chief feature of interest is that, although both birds play active parts in it (the flying-off and waiting of the non-diving bird is an active part, which culminates in the Grebe with a special display), yet the parts are different. If we may judge from the Grebe, either part

FIG 4.



Red-throated Diver: another sketch of an emergence ceremony.

may at different times be played by a bird of either sex. This is rendered more probable by the fact that the more active rôle on this occasion was apparently taken by a female.

3. A ceremony in many ways resembling the Plesiosaurus race is also common, but apparently only among birds which have mated up. It is always accompanied by a cry which is the same as, or extremely similar to, the "roll-growl" already described. The two birds swim, one leading, for some distance with their necks arched so that the tip of the bill is submerged. The bill is also held open, in order to give the cry. The bodies, however, are not submerged posteriorly, but kept in normal swimming position, and there is not a marked wave thrown off the breast, nor does motion appear to be at all violent. As in the Plesiosaur race, the birds may turn, and the former leader become the second. This ceremony might be performed on the small nesting-pools or on the lagoon. Owing to the snakey look of the neck when in this attitude, I shall call this the *snake-ceremony* (fig. 2).

There remain peculiar actions associated with coition; these, however, may best be described later, in connection with the account of a particular pair.

Activities of a Particular Mated Pair.

I will now proceed to describe in some detail the actions of one pair which I had under close observation for a few days, since I believe that in this way a fuller insight is gained by the reader (as it certainly is by the observer at the time) into the psychology of the birds.

On a small tarn about a mile from camp a single Diver was observed on June 30. The tarn was then only partially thawed, and nest-building was out of the question. It would appear, however, that the birds had already "staked out a claim" to this special nesting territory, as is known to be done by many if not all monogamous birds before actual nest-building begins (see E. Howard, '20). A single bird was again observed here on July 4; it was restless and remained on the tarn for a long time; nest-building had almost certainly begun, as the event showed. On July 5 both birds of the pair were seen on the tarn, and one visited the spot where the nest afterwards proved to be. It only stayed half a minute or less, and then returned to the water. The birds were continually giving a mewling call, very similar to that given by solitary birds on the water, or by sitting birds when man or a Skua threatens danger. The call as given on this occasion, however, I record as "louder, longer, and more emotional than when given by a solitary bird." Usually the two birds would howl almost, but not quite, simultaneously. There was certainly some sexual significance attaching to this "duet-howling."

At one moment the typical "roll-growl" was given. This I take as proof that a snake-ceremony occurred, although the birds were unfortunately invisible below the high bank. On my approach to pitch my observation tent, the birds rose together and made off. I take it as certain that no egg was as yet laid, since, once this has happened, the nest is sat on almost continuously to prevent Skuas stealing the egg.

Next day (July 6) I spent about 9 hours at the tarn. It was noticed that whenever the howl or mewling note was given, the neck was stretched out nearly or quite parallel with the water. This was confirmed on many subsequent occasions. The action seems to be inseparable from the particular note. It is probable that it renders the bird less conspicuous (see Van Oordt and Huxley, *loc. cit.*). The note was given repeatedly by the solitary bird (female) that was there at intervals from noon to 3 P.M. Occasionally the bill would be dipped as in sexual excitement. At one time she indulged in what were obviously practice dives, just in and out, emerging two to four lengths away. This was repeated five times in quick succession.

Shortly after, the male arrived. The female speedily joined him, and the pair swam towards me, the female leading, with bill slightly open. When close to the bank, the female suddenly performed a remarkable action, obviously of a sexually stimulating nature. She stretched her neck forwards at an angle of perhaps 30° with the horizontal, the head and beak also

pointing up, but at a less angle. The neck itself was straight and rigid. In this pose she swam close up to the male, crossing his bows, so to speak. Whatever its significance, the performance was exciting to watch. There was a tenseness about the bird's attitude, a rigidity, which has been commented on by other writers, notably by E. Selous, in connection with various sexual ceremonies in other birds (Selous, '01-'02, '05 *a*, '05 *b*). I can best describe the impression it made on me by saying that it was like that apparently produced by certain sexual dances of savage tribes—the whole thing fraught with the significance of sexual emotion, and mysterious in the sense of being thus emotionally charged far beyond the level of ordinary life, but completely natural and without restraint. It is fairly clear that, even in animals, the emotional tension during sexual excitement is far higher than at almost any other time, and that the impression given to the observer is, therefore, not wholly a subjective one.

On this occasion the male was absolutely unresponsive to the female's "stimulating" action. The pair went off together; after some time the female started to go by a long route across dry land to the nest, but soon gave it up. The pair then swam, the female again leading, to a little bar covered with moss on the far shore. This bar I afterwards examined, and found that on it there was a rudimentary nest, built almost entirely of the moss which was here abundant, both on the bar and under the surface of the shallow water near by. Another such "nest" was found on the shore of a second tarn on which a second pair was breeding. Very similar structures are built by the Crested Grebe; and in both cases their function appears to be the same—they are the places on (or near) which the act of coition occurs. Just before arriving here both birds simultaneously "looked into the water" (*vide supra*) for about 20 seconds; there was also a good deal of beak-dipping by both male and female. On arriving at the bar the female turned and gave an energetic splash-dive. The male responded by a less energetic splash-dive. The male then crawled out on the mossy bar, onto what I later found to be the pairing-nest; there he stood upright, stamped alternately with his two feet several times, and then sank down as if brooding. He plucked small fragments of moss in his beak, and apparently placed them round himself as if adding to the nest. The female meanwhile was swimming close to the bar, in water scarcely deeper than her draught, giving repeated splash-dives. Her tail (which of course was very short, as in all Divers and Grebes) was repeatedly waggled up and down. The association of this motion with copulation in birds is obvious and well-known. However, she did not land, but swam across to the right and back, giving several more splash-dives; the male got up and scrambled back into the water. The pair then went to the nearest point to the true nest, both diving twice *en route* (not splash-dives); the female led, at a fast pace. After one short abortive excursion overland towards the nest, followed by swimming off the shore, she

went right up to the nest and settled down on it. The male dozed on the open water with his head under his wing. It was remarkable that since the arrival of the male not a single sound had been uttered by either bird.

About half an hour later the male flew off. The female continued to brood. At one time a Richardson's Skua came down close to the nest. This was the signal for the Diver to give a series of mewling calls, with neck outstretched in the direction of the enemy. (Occasionally the neck may even be directed slightly downwards.) About 7 P.M. I went off to carry out some other work. On returning, she was on the tarn. I visited the nest, and found it a low heap of mud with a shallow depression, and a moderate amount of moss round the rim. There were also several pieces of slate on it, but it was not clear whether their presence was not purely accidental.

On my returning to the hiding-tent, the bird soon came back to the nest. At 7.45 P.M. the male came back to the tarn. The female continued to sit without making any sign for a few minutes, but then suddenly left the nest and joined the male. Both appeared excited, and "looked into the water" several times in quick succession. Immediately afterwards they both assumed a very poor "snake attitude," with the neck only slightly arched. This lasted but a short time; the female then gave five splash-dives in rapid succession. The pair then indulged in a snake-ceremony, swimming towards me almost parallel, neither markedly leading. It was, however, a poor affair compared with those at full intensity of emotion. They then swam close up to the moss-bank on which was the pairing-nest, the female leading; she swam close in and was obviously excited, but the male did not follow. After both had had a spell of rest on the open water, the male looked up and soon started a "roll-growl" (the first sound given by either bird since his arrival). The female soon joined in, and a typical snake-ceremony followed. They then returned, the female leading, to the moss-bank. The male scrambled out again on to the bank, but at the other end from the nest. He trampled as before, but less often, and settled down, but did not pluck any moss. The female, however, after first pecking at the moss on the bank, turned, put her head under water, and proceeded to pull large pieces of moss up from the bottom. These she then jerked backwards over her shoulder, dropping them carelessly into the water and showing no further interest in them. This she did eight or nine times in quick succession. After pecking up moss, both birds usually gave a sharp, emphatic shake of the head.

The male then got off, made for the shore near the true nest, and sat there some time on the mud. Then both came out onto open water, and a good deal of mewing in duet went on.

The female then led the way to the moss-bank, where (I quote from my notes) "she beached herself, stern just in water, breast on land, head down. The male followed, mounted onto her, standing nearly upright, and copulated or attempted to copulate (it did not look as if he was

successful, but this is hard to judge). He then walked up her body and off her right shoulder (in this whole action behaving very much like the Crested Grebe)."

The female remained perfectly motionless for one or two minutes, in the same extended position; the male, after sitting on the bank for a slightly less time, took to the water. The female then sat up, plucked up pieces of moss as before, but fewer and with less energy, and then joined her mate on the water. After swimming, with the male leading, they turned; the female gave a short flight of a few yards, the male swimming rapidly after her; the male then gave a similar short flight. Both shook their heads emphatically several times (compare the Crested Grebe). After a short time the female got up, followed at once by the male, and both flew off westwards and were lost to sight. This abandonment of the nest with an egg in it was remarkable; possibly they were more upset by the presence of the tent than they appeared to be. In any case, apart from the presence of a pair of birds which may or may not have been the same, for a short time next day, the tarn was abandoned, and the egg fell a prey to Skuas within 24 hours.

Another nest was discovered on a neighbouring tarn on July 7. This already contained two eggs, although this tarn had been still later in thawing than the other, and had ice extending for some distance in from all its margins on July 2. This tarn was within a short distance of camp, and the "roll-growl," signifying the mutual "snake-ceremony," was frequently heard from it (*e. g.* 5.30 A.M. July 9). This shows that mutual "courtship" continues, as in the Grebe, throughout the incubation period. On investigating the banks, a "cock's nest," similar to the one already described but rather more rudimentary, was discovered, also on a rather mossy part of the shore (as a matter of fact, the only mossy part in this tarn); doubtless it, too, subserved the function of coition.

The association of the mossy bar with the rudimentary nest is interesting. The true nest often contains some moss; and the behaviour of the female, above recorded, in plucking up moss from the bank shows that in the Diver, as in many other birds, the handling of nest-material has a sexually emotional association. It is presumably this emotional association which prompts the choice of a mossy bank as the site of the pairing-nest. There is, however, far less nest-material employed than by the Grebes; and accordingly nest-material plays a smaller part in the Divers' sexual ceremonies.

On my arriving at the hiding-tent on the evening of July 9, the female, who was sitting, was rather suspicious, left the nest, and swam about restlessly on the pool for some time. Although alone, she frequently dipped her head half into the water, as previously described, for 5 to 15 seconds. Thus this habit, which is undoubtedly the main "associational" habit of this species, may be associated with other emotions than that of sexual excitement—

in this case, with that of anxiety. It was here evident that it was performed especially when the bird was particularly nervous; for instance, whenever she approached the nest-region. This she did repeatedly, sheering off six or eight times before finally plucking up courage to ascend the nest. The "looking in the water" alternated with a curious action of the wings, first one and then the other being raised very slightly. This was not seen at any other time. The male arrived on the tarn about 6 P.M. The female flew along the water to his neighbourhood, uttering a repeated cooing note. Both made towards the nest, the female leading, swimming very low in the water and cooing; she made one short dive. Both then cooed in unison. No ceremony followed, however, and the female soon went on to the nest. The male shortly afterwards flew off, but returned within half an hour. No excitement occurred within the next hour. After this he several times came up close to the nest, and gave the cooing call, which was sometimes given by the female in response. Soon after this he flew off. Here we have evidence of sexual ceremonies in the morning, but a very "dull evening." Probably the mutual ceremonies are practised less and less as incubation proceeds.

Next day (the 10th) I was in the tent from 2.45 to 5 P.M. The male did not appear at all. The tent was now pitched at 6 yards from the nest. The bird was markedly less nervous than the day before, but every time that she approached the nest from the open water, she dipped her bill several times before venturing on the difficult overland traverse. This corroborates the interpretation of the "looking into the water" as an expression of emotion. On the 11th, the last day we spent on the Foreland, I spent 12.30 to 2 A.M. at this tarn. The male again did not appear. The female appeared to be sitting whenever I was watching; but there is no doubt that the male is to be found sitting in this species (Witherby, '00, &c.). During this period the three birds previously referred to (p. 257) flew down and, after circling round, alighted on the tarn. All were very alert in expression, and were repeatedly dipping their beaks into the water—*i. e.* under the influence of emotional excitement. From their sizes, I should say there were two females and one male. After a few minutes they rose, circled round again, and again settled. One separated from the other two. The (apparent) male of these two arched its neck very slightly, as if going into the snake position; on this, the other bird dived and emerged in the vertical "Penguin" attitude, as already described. The immediate fluttering over the water by the remaining bird on the female's diving indicates that this is a regularly-occurring ceremony and that the emergence was expected; the same is true in the Grebe.

The "Penguin" bird dived again, with a splash; but before it had emerged, the other two had both, for some unknown reason, flown off. The diving bird emerged in an abortive "Penguin" attitude, looked round to see

where the other was, and then it, too, rose and followed the others. They all three made off in wide sweeps, and were finally lost to view some miles away.

I take it that these three birds were not yet paired up for the season. Possibly here, as in the Crested Grebe (Pike, '13), some birds do not nest, but continue "courtship" actions throughout the season. The long flight to the tarn and away again so soon after is of interest; it may have been a pursuit; but, if so, it is interesting that the bird which took the chief initiative in courtship on the tarn was probably a female.

Other Observations on the Red-throated Diver's Courtship.

Before proceeding further, it will be as well to mention the actions observed by others in the same species. E. Selous ('12) made observations on a family in Scotland, during July, at a time when the young were hatched, and were being looked after by both parents. Although he was watching steadily for over three weeks, he only saw "courtship" behaviour on three occasions. This in itself is of interest, as showing that so long as the breeding-season lasts—*i. e.* at any rate so long as the instinct for caring for the young persists, and possibly until the autumn moult—the possibility of sexual ceremonies appearing in special circumstances will also persist. The observations of Pike ('13) are of interest in this connection. He states that a large percentage of the Crested Grebes on a certain breeding area, although mated up, failed, for some unknown reason, to build or lay in the season when he was there: these birds, and apparently none of the other pairs, continued their well-known mutual courtship late into the season (*i. e.* after the normal time for incubation was over). Facts bearing on this problem are well known in other species; for instance, in many birds, the final liberation of the parents from feeding the young, when these are old enough to look after themselves, is often marked by a recrudescence of various sexual activities. These are similar to the truly epigamic activities of the early part of the season, though they now, of course, have no function. Similarly, in birds which rear two or more broods, there is usually a recrudescence of epigamic ceremonies in the interval between broods. Looking at the matter from an opposite angle, we find that the song of many birds, *e. g.* the Nightingale, ceases immediately the young are hatched—*i. e.* as soon as the male embarks upon the new duty of helping feed the young. Mr. Eliot Howard informs me that in birds such as the Buntings, in which the males occupy territory long before the females arrive, the volume of song in the first period is greater than in the period immediately after the arrival of the females. This has been corroborated for other species, *e. g.* the Blackbird (Dewar, '20).

In a very similar way, the female, on reaching a certain level of endocrine stimulation, will permit and indeed solicit coition; her emotional activity will also find relief or expression in the building of the nest. Coition brings about egg-laying, and nest-building brings about the finishing of the nest;

a new period is thus introduced in which new objects are introduced to the bird. Her excitation, so far as it is determined internally, remains at the same level, but her activities are determined also by the objects presented, and she now begins to incubate. In the absence of nest and eggs she would revert to the behaviour of the preceding stage—coition and nest-building once more, as is shown by the behaviour of birds whose nest and eggs are destroyed after incubation has begun; but in the absence of the internal stimulation by the secretion of the gonad, she would neither brood, nor be eager for coition, nor build a nest.

The annual cycle of a bird is therefore divisible into a series of periods, determined (*a*) by the state of internal stimulation, (*b*) by external objects—the presence or absence of mate, eggs, young, &c. These latter will determine the division of the breeding-period into a number of sub-periods. In the third place, (*c*), an influence on behaviour is exerted by general environment—*e. g.* by the state of the weather, the abundance of food, &c.

So long, therefore, as the internal stimulation persists at the same intensity, the sub-periods will be mainly determined by the external objects presented to the bird. But, while any one sub-period will be characterized by one predominant type of behaviour, the other types of behaviour will be latent in the bird all the time, and may emerge under special circumstances, though rarely, so long as the breeding-season (*i. e.* the secretion of the gonad) continues.

To return to Selous's observations on the Diver. The male had just fed one of the chicks; he then approached the part of the pool where the female and other chick were swimming; the female also swam towards him. On the two birds coming to within a certain distance, both made two short flights towards each other over the surface of the water; each time the flight ended by the birds "as it were walking on the water, as a Penguin walks on the land, bolt upright, with the whole of the white expanse of the under surface . . . showing." It is like "a Penguin running a few steps, and then, for an appreciable period, standing upon the water, the naked legs and feet just hidden by it." On another occasion, the male of another pair was seen to alight on the water on its return from the sea, and to end its alighting in the following manner: it "footed it, for a little, towards another one, presumably its mate, . . . maintaining with the help of its wings the upright Penguin-like attitude."

On the third occasion, the female had started to give a special note with head stretched forward; she then began advancing towards the male in a series of little plunges. This stimulated the male to do the same. Each time the cry was given, the neck was arched and held rigid. They eventually met, and then quieted down.

It is interesting to note that none of the actions recorded by Selous are identical with those seen by me. This is probably due, at least in part, to

the different period at the time of observation. On the other hand, they are built up out of the same elements.

Bent ('19) says of all the species of Diver, as well as of numerous other Pygopodes, that they migrate in pairs, or at least arrive at the breeding localities in pairs, and select the nest-site as soon as possible. He believes they pair for life. In all species it appears probable that both sexes incubate (although from my personal observations it appears that one bird, presumably the female, takes much longer spells than the other; and see Turner, '13).

Courtney, quoted by Chapman ('22), gives a beautiful drawing of a common courtship ceremony of the North American Loon (*Colymbus immer*), in which one bird rises into the erect position, and runs along the surface of the water in this attitude for some way near another.

Bent (*loc. cit.*) refers to the "maniacal" screeching laughter of this species in the breeding-season.

Seidlitz ('13), writing of the Black-throated Diver, says that each pair has a well-marked and large territory (*Revier*). He states that there are as many unpaired as paired birds; these are birds of one, and possibly of two years of age. He does not mention whether these ever indulge in "courtship" ceremonies. This would be a point of considerable interest.

Bahr ('07) mentions the dipping of the beak into the water when the bird is nervous and afraid to return to the nest. He also, on one occasion only, saw a very remarkable performance by a single Red-throated Diver. The bird ascended to a great height, and then descended headlong, twisting and turning as it did so, the air rushing through the feathers, making a noise "like a train." Such descents are, of course, well known in many birds, *e.g.* Rook. They are common in Louisiana Heron, Little Blue Heron, and Snowy Egret on returning to their rookery, and I have on one occasion seen a somewhat similar performance by our common British Heron. It is probable that these actions should be classed as play, and not as courtship.

Hatch, quoted by Bent (*loc. cit.*), states that *C. immer* has a remarkable family habit. When the young are (apparently) well-grown, they sleep with their parents on the pool. In the early morning, before sunrise, the male parent gives a special call; all draw near, and, after a little manoeuvring, start to run over the water side by side in a line "at incredible speed," with the wings about a quarter-extended, the whole motive power being derived from the feet. They run thus for about 400 yards, then wheel, and return to the starting point. This is repeated several times and suddenly stops. It would be interesting to have further observations on this extraordinary ceremony.

INTERPRETATION.

It will be seen from the above that (as in many, and indeed in most, of even our commoner birds) much remains to be known about the life-history

and especially the relations of the sexes. Those who have opportunity, patience, and a good glass, and are willing to take full notes, will find that steady observation of almost any species of bird at the beginning of the breeding-season, particularly if a single pair can be followed throughout, will bring results which may be of very considerable interest, both from the standpoint of pure biology and also from that of comparative psychology, as well as being in itself a very fascinating occupation.

The following paragraphs must therefore be taken only as a provisional interpretation of the observations which have so far been recorded.

The Red-throated Diver is monogamous; possibly it pairs for life. If it pairs for life, it follows that the pairs will have some form of association even through the winter. In any case, however, a change occurs in spring. Either the loose association of male and female is replaced by a much more intimate one, or else the birds have been really unmated during the winter, and now do separate out into pairs. This must, of course, be the case with birds which have not previously mated. In any event, the change is definite, and warrants the term "pairing-up" which is usually given to it. This change is presumably associated with a change in the reproductive organs, which start to secrete their specific hormones.

The pairing-up appears, at least with some individuals, to occur in the winter haunts. When so, it is followed, probably shortly, by migration, in pairs, to the breeding-grounds, where each pair as soon as possible stakes out a territory for itself. The present species appears to breed on small pieces of water, and probably the territory is, in most instances, coterminous with the nesting-pool.

The fact that the pair migrate together and choose the nest-site and territory together is in strong contrast to the occurrences in such Passeres that have been fully investigated, such as the Sylviidæ and the Emberizinae, in which the males alone stake out territory (Howard, '20), and, if migration occurs, migrate before the females. However, it seems to occur in many *Pygopodes* (Bent, *op. cit.*); and in Herons (unpublished observations of my own), although migration is in flocks, the choosing of the nest-site is undertaken by the pair together.

Although from the evidence of others it appears certain that pairing-up may occur before migration, yet my own observations appear to point to this not being universal. The fact that the "Plesiosaur" ceremony occurred frequently during the first few days of our stay, but later was absent or very rare, as well as the fact that the simplest interpretation of it was that it was concerned with the "choosing" of mates, indicates that probably a good many birds arrive unmated on the breeding-grounds. Possibly (I throw this out merely as a suggestion) the birds which have nested before, pair up in winter quarters, while those which are about to nest for the first time do not do so until they arrive on the breeding-grounds.

The "Plesiosaur" or "race" ceremonies, then, appear to be competitions for a mate. It is of interest to find that when three birds are participating in these ceremonies, their respective sizes indicate that they may be either two males and a female or two females and a male. This is in accordance with the rest of the facts observed about courtship in this species—the two sexes appear to play almost identical (or interchangeable) rôles.

The only occasions when I observed the dive followed by the "Penguin-like" emergence, also seemed to be in this *pre-mating* period. The erect "Penguin" attitude, however, as Selous' observations show, is not only confined to this period, although he does not record diving followed by this attitude.

There is, however, another possible interpretation of the participation of three and four birds in these ceremonies, which may be best understood after a brief digression. In the Buntings, as Mr. E. Howard kindly informs me, during the period while male and female are both present on the territory, but coition and nest-building have not yet begun, every day begins in the same identical way. The male wakes first: later, the female emerges too from her roosting-place: after a short time the male flies at her, eager for coition. She however flies off, and there follows what Howard calls the "sexual flight," when the female, dodging and twisting, is pursued closely in her rapid flight by the male. Eventually the birds seem to get exhausted, and alight. Such pursuit flights are of course well known among many species. What is of special interest, however, is the fact that once the flight has started, it is a source of great excitement to other males in the vicinity, and, although these males may have been long in occupation of territory, and mated, yet one or more will usually join the rightful male in the pursuit. In passing, it should be observed that this instinct of other males to join in the excitement of these pursuits appears to be at the bottom of those undignified skirmishes of the House-Sparrow, in which a single unwilling female is mobbed by a number of males; and see also Bent, *op. cit.*, pp. 186-191, where the Californian Guillemot is described as becoming very much excited at the sight of an act of coition by another pair.

It is conceivable that the Plesiosaur race of the Diver may be a mutual "post-mating" ceremony, essentially identical with the "snake-ceremony" described as occurring later in the birds' history, but, since it takes place before the nest is built and other activities share the birds' mind, differing in its greater intensity. If so, then the participation of three or four birds in the ceremony may be due to others joining in under the influence of excitement—others which are either wholly unmated, or else are mated but temporarily without their mates. Since there were almost always several birds on the lagoon, while the nesting-pools hardly ever had more than a single pair on them, and since further the greater level of emotional excitement in the Plesiosaur ceremony is unmistakable, it would be quite intelligible that the threes and fours were only seen on the lagoon, and only performing in the Plesiosaur, not in the "snake" ceremony.

For the present, however, I prefer to think of these as ceremonies actually connected with mating-up. If so, they are interesting, as they would be, so far as I know, the first pre-mating ceremonies described which were "mutual," in that both sexes played similar rôlés. Further observations are urgently needed, not only on this particular point, but on the whole problem of pre-mating ceremonies, especially in species with mutual post-mating courtships.

In any case, the *post-mating* ceremonies are essentially mutual. The commonest is the "snake" ceremony, the incentive to which may, to judge from my observations, be given by either sex. This ceremony, like the pre-mating ones, may often be "self-exhausting" in the sense that, as in the Crested Grebe, it need by no means always or usually lead to coition, but may be followed by a relapse into ordinary non-sexual routine. Here, however, I should like to put on record that further observation on this species and on Grebes has convinced me that such ceremonies may often have a stimulative effect, although that effect may be gradual and in a sense cumulative. It is very common in the Grebe to see a pair repeat a series of mutual ceremonies at frequent intervals, and finally go off in the direction of the nest and pairing-platform; this has also been observed in the same species by Selous, and clearly occurs to some extent in the Red-throated Diver. That in certain circumstances the ceremony may be completely self-exhausting is perfectly intelligible: like the song of most Passeres, the performance of the ceremonies is definitely pleasurable in certain states of emotional tension. Physiologically, it is then performed "for its own sake": it may or may not, according to various circumstances, have the further biological function of raising the emotion to a pitch at which coition is desired.

On the other hand, there is no evidence that in the Divers there exist special attitudes and ceremonies especially used as a symbol of readiness to pair, as in the Grebe. The approach to the pairing-platform is in itself a symbol of some degree of readiness to pair. The emotion associated with this may apparently again be dissipated by excited actions, such as the pulling of weed from the bottom, and by the ascent of the pairing-platform without actual coition.

The situation of the pairing-platform in a mossy situation is of interest. Moss is often but apparently by no means always used as nest-material, and in any case always in very small quantities; the birds can never handle it in such large amounts during nest-building as they do in the vicinity of the pairing-platform. Two hypotheses might be considered in regard to this. In the first place, it might be a reminiscence, the birds having in the past employed more moss in nest-construction than at present. Or it might represent a specialization; once the divergence between nest and pairing-platform had arisen, and the emotions connected with coition had become attached exclusively to the latter, new ceremonies, based on the handling

of nest-material in the first instance, might have been developed in association with the pairing-platform to a much greater pitch than they had ever been formerly. If this is so, and offhand I am inclined to accept it as the more probable, there has been an evolution of the pairing-platform and the ceremonies connected with it, which is in many ways similar to that of the Bower-birds' bower.

Personally I have not seen nearly so many post-mating ceremonies in this species as are to be observed in the Crested Grebe. This is undoubtedly due in part to the paucity of my observations. The work of Selous shows that "Penguin" ceremonies do occur in this period, and, it is interesting to note, continue, though rarely, after the young are hatched. Thus the physiological state (presumably dependent on gonadal secretion) during which epigamic ceremonies can be performed extends, apparently in all birds, up to the very end of the breeding-season; it does not then issue so frequently in "courtship," because incubation and the care of the young afford other outlets for physical energy and emotional tension.

On the other hand, only three, or possibly four types of epigamic ceremony, whether pre- or post-mating, have been observed at all in this species, whereas in the Grebe six have been seen; and the greater abundance in the latter is probably not only apparent but real, and associated with the greater development of epigamic ornament in the Grebe.

Incubation appears to be undertaken mainly by one bird, the smaller of the pair; but there are numerous records of males also incubating, and it is probable that in the Divers, as in other forms with mutual courtship, there is a sharing of the duties of incubation as well as those of caring for the young. It is noteworthy that no ceremonies associated with nest-relief have been observed in the Divers or Grebes, whereas they are common in Herons (my own observations), Pelicans (Chapman, '08), &c. It would be important to find out the range of size in male and female Divers. I am inclined to believe that a single bimodal curve would be obtained. For a discussion of sex-difference in birds with close similarity of male and female, see Huxley, '22 *b*.

GENERAL DISCUSSION.

It remains to discuss some of the general significance of such forms of mutual courtship as are seen in the Divers, Grebes, Herons, and Egrets—to mention only birds whose sexual habits I have myself investigated.

As I have recently pointed out (Huxley, '21), it is impossible in the present state of our knowledge to maintain that Darwin's original theory of sexual selection is adequate to explain the origin of most of the sexual ceremonies and adornments to be found in monogamous birds. These adornments are chiefly used in ceremonies which take place *after* mating-up has taken place for the season. There cannot therefore be a direct selection as between one male and another in respect to them. It may be mentioned

in passing that there is evidence of this direct competition (using the word in a metaphorical sense) between males in at any rate some polygamous species, *e. g.* the Blackcock (Selous, '09). What, then, is the function of the sexual adornments and ceremonies—for the most casual observation is enough to convince anybody that they possess *some* function?

It is to be observed that sexual ceremonies and colours or structures which are displayed solely or chiefly during such ceremonies are only to be found in animals of a certain grade of nervous organization. Observation on newts, which are remarkable in that the males deposit their sperm in the form of spermatophores first and afterwards go through their display ceremonies, indicates that the function of the display is a stimulative one, designed to stimulate the female to pick up the spermatophore (quoted in Pycraft, '13). The experimental work of Sturtevant ('15) on *Drosophila* entirely corroborates this view. The male in this species performs special actions with his wings when "courting" the female. Sturtevant found that males with the wings cut off, when imprisoned singly with females, succeeded in copulating, but after a longer time than normal males in a similar situation. On the other hand, when each female was placed with two males, one normal, the other with amputated wings, it was found that the wingless males were successful in copulating almost as often as were the normals. This can only be interpreted to mean that the wing-waving ceremony stimulates the female in such a way that she is then ready to receive *any* male in copulation. Morgan ('19) appears to adopt this attitude in viewing the whole sexual selection problem, but his statements are not very definite, and he does not bring first-hand observation to bear on the question.

Observation of most of the post-mating courtship ceremonies of birds bears out this interpretation. If we for a moment confine ourselves to a consideration of birds with distinct sexual dimorphism, either of colour and structure, or at least of behaviour, we can say (1) that the female is always or usually at a lower level of sexual emotion than the male; (2) that the nervous organization of birds is so advanced that behaviour is no longer merely reflex, but that it depends in the main on highly-developed instincts, each associated with a particular emotional tone. The centres for the instinct require to be stimulated before the impulse to the particular instinctive action is felt; there is a certain minimum intensity of stimulation necessary, which, as we have just said, is, in the case of the sexual instinct, generally higher in the female than in the male; (3) that, accordingly, a necessary preliminary to coition is the raising of the emotional state of the female to the level at which her sexual instinct is stimulated to action.

If we like to sum it up from a slightly different angle, we can say that in birds (as well as in other groups), mental organization has reached a pitch at which the higher centres concerned with emotion play a predominant part in

determining behaviour, and that a stimulation of the emotional centres is a necessary preliminary to coition. In a precisely similar way, at an earlier stage of evolution, a stage of general bodily organization was reached at which internal fertilization was desirable or necessary. On this stage being reached, it became imperative that coition should occur, and that, in practically all cases (the majority of birds constitute an exception), specialized copulatory organs differing in the two sexes should be developed. Both (*a*) copulatory organs and (*b*) most of the courtship ceremonies and epigamic structures we have been considering can therefore be classed under the same head—viz. as accessory sexual organs. I have heard this point epigrammatically summed up in discussion by the remark that this type of male courtship is a “psychological penis.” In any event, it is clear that just as no one has ever considered it necessary to postulate a *special type* of selection to account for the origin of copulatory organs, so the origin of courtship, so far as it is of this stimulative type, does not demand the special evolutionary mechanism of Darwinian sexual selection to explain it.

The question may now be raised as to the relationship between this “stimulative” courtship in species with sexual dimorphism and courtship in species where the appearance and behaviour of the sexes are similar. To answer this we must go back for a moment and ask a more fundamental question:—What is the reason, in the dimorphic species, for the difference in sexual excitability between male and female? There may be some primary difference between the sexes which tends in this direction, but there can be little doubt that the marked accentuation of this, which is seen in most dimorphic species among the higher animals, has for one main function, as has been several times suggested (*e. g.* especially by Groos, '98, and E. Howard, '07-'14), the *regulation of coition*. If both sexes were highly excitable, coition would occur too often; on the other hand, it would be undesirable to reduce the strength of the impulse too far, until it was near the lower level at which it ran the risk of being extinguished under the pressure of accidental unfavourable circumstances. (There is much evidence to show that, *e. g.*, cold and damp have a markedly depressing influence on the sexual activity of birds.) An obvious method of ensuring the golden mean between the danger of excess and that of possible suppression of the instinct is to have one sex with a very strong instinct, or at least one which is readily excitable, while that of the other requires considerable stimulation to arouse it. (We have already seen that the instinct must be aroused through stimulation of the higher centres.)

There is, however, another method of ensuring a similar result, and that is to have the sexes at the same general level of excitability, the male less excitable than in dimorphic forms, the female more so. In this case both sexes will constantly be reaching the level of stimulation at which desire for coition occurs. On the other hand, here again it is unlikely that both will at the same moment spontaneously reach this level—unless both were

keyed so high that an undue amount of coition resulted. Further, when the level of readiness to pair is reached, it does not follow that the bird will be under that amount of emotional tension which results in some physical expression being necessary: in fact, this appears to be the accompaniment of a definitely higher level of excitement. "Courtship" ceremonies which result in these circumstances may therefore have one of two functions. In the first place, they may be performed by one alone; they may then convey to the other that the first is ready to pair—in other words be *informative* in function—or in addition be *stimulative*, and help to key the other up to the requisite pitch. The stretching-out in the passive pairing attitude which occurs on open water in Crested Grebes (Huxley, '14) and on the nest in Dabchicks (Selous, '15) appears to be primarily such an informative symbol, although it is at least probable that it is also stimulative. On the other hand, there are many other courtship actions, such as the majority at least of the mutual post-mating ceremonies described both for the Diver and the Grebe, which appear to be primarily, or in any case, primitively stimulative in function. They are not symbolic, in the sense that they are not representations of coition attitudes, and both birds take part in them, usually though not always performing similar rôles. These have as their original function the raising of the level of sexual emotion—only here it is a mutual raising of an originally similar level. It is true that, as in the Grebe, these ceremonies are frequently what I have called self-exhausting, and do not lead to coition, but this is probably secondary; it is also probable that they may have other functions besides that of stimulating to coition. Both these points, however, we must discuss later, as also the reason for the existence of the two different methods of dimorphic and of mutual courtship.

It is no doubt often difficult to distinguish between the two; but in the Crested Grebe at least there appears to be a real distinction. Objectively ("behaviouristically"), *e. g.* the pairing-attitude is adopted only near the nest or pairing-platform, and is almost always followed closely by coition; it is not accompanied by any of the usual signs of violent nervous activity, nor by anything that can be called display. *Per contra*, the mutual ceremonies may take place anywhere, may or may not be followed by coition, and, if so, generally after some interval; they *are* associated with various signs of general nervous activity, and *do* serve to display special structures and colours.

Psychologically, it would appear that the coition-attitude is narrowly and specifically associated with coition, and is "informative," denoting readiness to perform the act itself; while the mutual display ceremonies are not associated with coition in particular, but with general emotional excitement. In so far, therefore, as they have a stimulative function, it is concerned with raising the general emotional level to the pitch required to make the birds repair to the neighbourhood of the nest—*i. e.* to bringing about the general

psycho-neural state *within which* the particular state of readiness to perform the act of coition itself can only occur.

In so far as they are truly self-exhausting, and not stimulative, they must either be considered as biologically functionless, as so many by-products of a mental organization of the type required to execute the stimulative forms of display (*cf.* the way in which song has in many cases become a biologically useless outlet for very various emotional states, as well as subserving its primary functions in connection with territory); or, as I have previously suggested (Huxley, '14), their function must be concerned with keeping the pair, in species in which both sexes share the duties of incubation and care of young, more closely attached to each other throughout the season.

Here we must be content to note that both types are "accessory" sexual characters; in the sense that their main function, like that of copulatory organs, is to facilitate the union of the gametes, and that they represent different methods of arriving at the same result—*viz.*, the raising of the emotional level of the pair to a point at which coition will take place.

It may be suggested that to speak of excessive coition, as I have done, is to use a phrase which it is difficult to justify biologically. It should be remembered, however, that experiment has shown that, in mammals at least, a male will, if females in the right condition are provided, continue to pair until his seminal fluid contains very few spermatozoa (Hays, '18; Lloyd-Jones & Hay, '18). Normally, of course, this is prevented in mammals by the fact that the females only attain the condition in which they are ready for coition for very short periods at a time. A further disadvantage would accrue from the absorption of attention in the sexual act which is so marked a feature in most animals. The more frequent this might be, the more the species would be exposed to the attacks of enemies. The whole subject has been fully dealt with by Groos in his interesting book 'Die Spiele der Tiere' ('98); and see also Mottram ('14).

The regulation of coition, however, is undoubtedly not the only factor of importance in the evolution of courtship. Previous workers on the subject have been too exclusively preoccupied with the epigamic significance of courtship. This was natural; but they should have remembered that the organism is a whole. We find as a matter of fact that the form and extent of courtship, nay, in some periods its very existence, is due to causes which are not epigamic in origin, but connected with other fundamental biological needs in relation with the annual cycle of the animal.

In many birds, as we shall find (see Howard, '20), it is of prime importance for the welfare of the pair and its offspring that a well-defined territory shall be occupied in which the nest is afterwards built, and from whose produce the young are usually fed. It is a biological advantage to occupy territory early; birds which did not do so until late would find all available space taken up, and would have to fight for occupation. When the sexes are dimorphic, one will usually be the more active in this task—almost invariably

the male. But once he has occupied the territory, it will be again a biological disadvantage for the female to put off too long her quest for territory-plus-mate, or else she too will find herself forestalled.

On the other hand, the exigencies of the food-supply demand that oviposition should not occur until a certain date, varying naturally for different species, but almost always considerably later than the date at which territory is occupied. Thus we have two opposed advantages—one in the early occupation of territory, one in the late starting of coition. As a result, there will be a period after both birds are on the territory—*i. e.* after pairing-up has occurred—when it will be biologically undesirable that oviposition should occur. This we may call, if we choose to adopt a not wholly suitable human metaphor, the “engagement period.” Extremely little is known concerning this period in species with mutual courtship: in many of them it is absent, the birds only returning to the breeding-grounds, or only pairing up, immediately before coition can and does occur. (This is apparently the case in Snowy Egret, Louisiana Heron, and many cliff-breeding birds.) In any case, what is known is so slight as to make discussion unprofitable.

In many dimorphic species, on the other hand, a good deal is known. Such an “engagement period” occurs apparently in all small Passeres which have nidicolous and insectivorous young, and which therefore, as Howard has demonstrated, imperatively require a territory which is not merely a nesting-area, but a hunting-ground from which the needs of the new-hatched young may be supplied. As we shall see later, the dimorphism itself has probably been evolved in relation to other biological needs of the species—*viz.* the necessity for concealing coloration and behaviour in the female. Here, however, we shall take the dimorphism as given.

The simplest way of satisfying these biological requirements is to make the male enter in early spring on to a sexually-excited state in which he is impelled to seek and occupy territory, to pair or attempt to pair with any female who stays in the territory, to assist in feeding young when hatched, etc. So far as his endocrine excitation goes, he remains in the same phase throughout the season.

With the female, however, the case is different. She must pass through at least two phases of excitation—the first sufficient to impel her to abandon the “neutral” non-sexual existence of the winter and to seek and if necessary fight for (Pl. 15. fig. 7) the company of a particular male, but not sufficient for coition to take place; the second, more intense, impelling to coition and nest-building; when the eggs are laid, to incubation; and, later still, to the care of the young.

There will thus exist a period in which the male will be anxious for coition, but the female will not permit it. Further, the biological causes for the existence of such a period are not epigamic, not concerned with the relation of the sexes, but are to be sought in relation to the need for occupying

territory and the need for nesting at the proper time for supplying the food-requirements of the young.

Such species, where territory is of major not of merely minor importance (*feeding territory* as opposed to merely *nesting territory*), we may for convenience call "territory birds." In them, during the female's second phase, there is comparatively little "courtship" on the part of the male. When the female feels impelled to coition, she adopts a particular attitude, and the male immediately performs the act. The bulk of the "courtship" (excluding song) is due to the fact of the existence of the "engagement" period when the male and female are in different states of endocrine excitation, and this is a biological "accident" arising as a by-product of other needs and functions.

The song, on the other hand, is, in territory birds (where it reaches by far its highest development), connected primarily with territory—with attracting females to, and warning other males off, occupied areas. The displays and pursuit flights are merely an expression of the desire of the male for coition, a desire which cannot be satisfied in the engagement period. The display is in origin an adoption of the coition attitude itself, or something closely resembling it, brought about naturally as a result of brain-structure when a certain level of sexual excitement is reached; the pursuit flight is in origin an attempt to force the female to submit to coition.

Once, however, these actions had arisen in this way, they formed a possible basis for further evolution. The fact that in large numbers of species of this type the male is brightly coloured, and brightly coloured in such a way as to display the bright colours in the above-mentioned type of ceremony, is evidence, though of a merely circumstantial kind, that something of the sort has occurred, and that the ceremonies, originally mere attempts at coition, have later acquired a second and presumably stimulative function. The fact that the males of some territory birds are not brighter than the females (*e.g.* the Warblers) may well be accounted for on the supposition that in these species protection is desirable for both sexes.

There is, further, interesting evidence to show that these ceremonies probably do possess some stimulative function.

I am informed by Mr. Howard—and the statement has been in general corroborated to me by Mr. Jourdain and other field ornithologists—that in seasons when the weather has been very cold and unpropitious during the time of egg-laying and immediately before, the average number of eggs in a clutch is smaller than usual, and that the proportion of infertile eggs is higher than usual. This latter effect may in part be due to actual damage to fertilized eggs soon after laying, caused by the inclement conditions; it may also be due to failure of fertilization. The smaller number of eggs in a clutch must be due to failures in ovulation. It is further well known that ovulation in birds is, in part at least, under nervous control; the caressing of a female virgin dove on the back of the neck with the hand causes ovulation.

Harper's observations (discussed by Marshall, '22, pp. 134-135) make it clear that the female pigeon will not ovulate unless stimulated emotionally. This stimulus is normally provided by the male; but two females isolated together will often lay. Single females when isolated never lay (except occasionally when overfed, and then only a few eggs). The recent work of Chance ('22) indicates that in the common Cuckoo ovulation occurs under nervous control, the sight of a pair of foster-parents building their nest acting as a stimulus. It is obvious, further, that the willingness of female birds for coition is not almost exclusively a matter of internal secretion as in mammals, but is largely under emotional control. It is also well known to field observers that the state of the weather has a marked effect upon the emotions and their expression in birds; song and display is regularly far poorer on a cold, dull day than on a bright, warm one. Other things being equal, therefore, anything which tends to counteract the depressing effect of bad-weather conditions upon the emotions and the actions under their control will be of biological advantage in that the number of ovulations will be increased, and also the number of coitions, and so the chances of fertilization for the eggs after ovulation. There would thus in ordinary seasons be no marked biological advantage gained from stimulative ceremonies; this would accrue in exceptionally bad seasons only.

It appears, as I have already indicated, that in birds with mutual courtship the ceremonies do have a stimulative effect, although this is usually of a general and indirect kind, keeping the level of sexual emotion up to a constant pitch, and occasionally heightening it so that visits are made to the pairing-platform, &c., where coition will usually occur. It is highly probable that a similar general stimulation is exerted by the more primitive displays of the "territory" birds, although here the stimulation is not mutual but unilateral.

It is further clear that any display which did have such an effect would reap the biological advantages, mentioned in the preceding paragraph, of counteracting the bad effects of cold seasons. As a matter of fact, even in these bad seasons some nests will be found with full clutches of eggs and normal proportion of fertile eggs. There is, therefore, a form of natural selection actually in progress here, which (as often) is only operative in particularly adverse conditions.

It is of very great importance that this point should be cleared up, and that field ornithologists should undertake careful statistical work on the relation between weather, number of eggs in a clutch, and percentage of infertility. It is only so that firm bases can be found for biological theories.

It must now be asked, as regards stimulative displays, what form of stimulus has been adopted and why. So far as males of dimorphic species are concerned, what is the position? It is that they are subjected to a mental state which is comparatively rare in organisms below man, of being stimulated by a powerful emotion but being unable, so long as the female

remains passive, to express it physically by the natural channel proper to the instinct which it accompanies. What will the consequence be? It will be that the psycho-physical energy will discharge into other motor channels, since it is debarred from discharging into its proper and normal channels.

Perhaps the most frequent way in which it is discharged in birds is by rapid, restless movement, accompanied by drooping and partial spreading of the wings, spreading of the tail, and erection of feathers, especially on the head and breast. This type of action seems to have had a dual origin. In the first place, it is often very similar to the actions normally adopted at coition, *e. g.*, as Mr. Howard informs me, in the Buntings. In the Warblers the similarity is still marked, but to a lesser degree. As I have suggested, it is probably the direct result of the unsatisfied desire for coition. In the second place, however, it appears to represent the result of a general state of excitement, quite apart from any representation of coition attitudes. It is often difficult in any particular courtship ceremony to disentangle the share of the two contributions. In the Grebe, for instance, the ordinary ceremonies are in no way representations of coition actions, while in the Buntings they are almost wholly so. In any event, the dual origin of the ceremonies as a whole is clear—general expression of hyper-excitation combined with more or less of the typical coition attitudes.

Once this type of action exists, however—and it will inevitably come into being in some form or other in the conditions which we have outlined,—it will naturally form the chief basis for the development of specialized courtship actions and courtship colours and structures belonging to the stimulative type. When it is the wings and tail which are spread and the crown and breast-feathers which are erected, it will be inevitable that, if further stimulation is advantageous, it will in the main be achieved by making these parts more conspicuous (so as to accentuate the difference between the normal appearance of the bird and its appearance under the influence of sexual emotion); and this will be most readily done by the development of bright colours on these parts, or by the formation of special structures in these regions—structures which are usually displayed in full only under the influence of sexual emotion. Since the form of the wings cannot be much altered without interfering with the efficiency of flight, it follows that special courtship structures will not often be developed in connection with them; and as a matter of fact we find that the chief special courtship structures are crests on the crown (as in Peacock, Herons, Golderest, Peewit, Cranes, &c.) or breast-plumes or other structures on the breast (as in Herons and Egrets, Bustard, Umbrella-bird, &c.), or elongations or other specializations of the tail (*e. g.* Pheasants, Humming-birds, Blackcock, Lyre-birds, &c.) or of the tail-region (Peacock, &c.).

The erection of feathers on other parts than crown or breast is also common, and its specialization gives us structures like the ruff of the Crested Grebe and that of the Ruff, the elongated scapulars of Herons, and those, both

elongated and dissected, of Egrets, together with some of the peculiarly situated plumes of Humming-birds and Birds-of-Paradise.

It appears, then, that "courtship" consisted at first chiefly of non-significant movements employed by the male as an outlet for the pent-up sexual emotion, these being in part derived from those employed in coition, and that special colours and structures displayed only mainly during these movements are later specializations. If so, then we should expect to find some species of birds in which the movements exist, but not the special colours or structures—"courtship" actions without epigamic colours or structures. This is as a matter of fact the case. The Sylviidæ, for instance, give us many examples of species which are not dimorphic in colour, or only so to an obviously non-significant extent, but are dimorphic in behaviour, usually the males alone performing special post-mating ceremonies, apparently stimulative in function, in which wings, tail, and feathers are moved in the general way that has been described (E. Howard, '20). Rarely, however, both birds perform ceremonies simultaneously, as is shown in fig. 8 (Pl. 15). But the two perform ordinary unilateral ceremonies, and not in any common rhythm. There is no sign of a unified mutual ceremony. It is an interesting intermediate type of behaviour.

Usually, however, the close observation of the courtship of a species reveals other behaviour which cannot be brought under the rubric of originally non-significant physical release of emotional tension. I refer to actions which are to be thought of as having originally been developed in connection with certain other functions, and later having been connected with sex in courtship displays. Such actions have already been referred to. Sometimes they are to a certain extent associated with sexual emotion, as are all those connected with nesting-material; sometimes they appear to have no such connection, such as the preening, head-shaking, dipping of the bill, &c., which we have noticed in Divers and Grebes. In Mute Swans, I recently observed some interesting courtship-actions, and there one of the prominent pieces of behaviour was the dipping of the whole head and fore-part of the body below the water; the action was strongly reminiscent of an incipient attempt at reaching down to feed in the characteristic swan manner. The birds also repeatedly preened themselves in a manner very similar to that seen in the Grebes—*i. e.* a manner indicative of the action being used in what I may call a ritual way, and without any of its usual functional significance. I am confident that when once attention has been drawn to this "ritual" use of non-sexual actions during courtship activities, it will be found to be of very wide occurrence. Prof. H. Balfour informs me that it occurs commonly in the Gannet. The association of nesting-material with courtship is certainly very widespread, and here we may probably see the working of direct association. The sexual emotion directly activates the centres connected with nest-building and the handling

of nest-material, because the two activities have been so often actually connected. But we cannot adopt this comparatively simple explanation for the incorporation of wholly non-sexual activities, such as preening, in courtship. So far as my personal experience goes (and so little attention has been devoted to the matter that the literature is of scarcely any help), the birds which make most use of these non-sexual actions in courtship are those which make least use of the peculiar expressional movements of wings, tail, and feathers generally, which we saw made up the raw material of courtship actions in most species. If this should turn out to be generally true, then we should have to suppose that the emotional tension, since for some reason it does not in these birds express itself in the originally non-significant methods of general wing, tail, and feather movements, must find an outlet elsewhere, in the guise of actions which are already performed by the species in other connections. In any case, it is clear that these actions are utilized, like the general non-significant actions, as physical relief or expression for emotional tension; and that since they are already given in the bird's instincts and habits, they form the natural raw material—the natural outlet for surplus psycho-neural excitement due to emotion temporarily unable to find its normal expression.

In a sense, therefore, the non-sexual associated actions are mere expressions of emotion, comparable to the meaningless acts often performed by men under the influence of great emotional tension. But once they have come to be associated with sexual emotion, they then become the raw material which can be worked up into more elaborate courtship ceremonies. Such, for instance, appears to be the origin of the head-shaking ceremonies in the Crested Grebe. In diving birds generally, there is an almost universal habit of shaking the head on emerging after a dive. This is, as we have seen, slightly associated with sexual emotion in the Diver, but in the Grebe the head-shaking is a very elaborate part of highly-specialized ceremonies, and its origin from ordinary non-sexual head-shaking can only be deduced from indirect evidence. Unless, however, its origin be of this nature, it remains quite obscure.

The association of diving with courtship in both Grebe and Diver may be adduced as further proof of our contention. The special "splash-dives" in the Diver, and the emergence from the water in a vertical attitude which occurs in both species, are both obviously modifications of the ordinary diving practised for food, which have now an exclusively emotional significance, and a sexual function. Under the influence of unsatisfied sexual emotion the bird indulges in various forms of action habitual with it; later, specialization has taken place so that the sexual modes of diving become quite different in appearance from the original non-sexual mode.

As a matter of fact, when we survey the varieties of courtship, we find that they are not uncommonly to be regarded as specializations of normal

activities of the species. For instance, various hawks (*e. g.* Kestrel and Peregrine) have courtships which are based upon the wonderful powers of flight possessed by the group; while many water-birds, like Grebes and Divers, show courtships in which some normal aquatic performance is sexually utilized. Thus in considering the genesis of courtship ceremonies, we have to distinguish between the raw materials and the later specialization. The raw materials are (1) coition-attitudes; (2) originally non-significant general movements, especially of feathers, wings, and tail; (3) actions originally connected with activities in themselves associated with sexual emotion, such as nest-building; (4) actions originally subservient to some non-sexual function.

Later, specialization consists (1) in the development of striking colour on parts prominently displayed in the raw actions; (2) in the development of such parts to form special structures (*e. g.* tail-coverts of Peacock, ruff of Crested Grebe).

The difficult question remains as to the reasons for the existence of dimorphism of courtship in some species, but of mutual ceremonies—associated, be it remembered, in the majority of species, with special colours and structures of as definitely sexual (epigamic) significance as in dimorphic forms—in others.

In general, it appears that it must have some connection with mode of life, although in the absence of detailed information on many birds, and of statistical treatment, our conclusion cannot be wholly satisfactory at present. In the first place, it is undoubted that polygamous species present the most extreme cases of male adornment, combined with protective colouring in the females. Secondly, in monogamous species with marked male adornment, the females are usually protectively coloured, and usually undertake the whole of the duties of incubation—*e. g.* Anatidæ, such of the Pheasants as are monogamous, &c. In some forms with dimorphic courtship, such as the Sylviidæ, the two sexes are often not very distinct, and are both more or less protectively coloured; both sexes may incubate here, although the female does so much more than the male. The Sylviidæ may be regarded as primitive in respect of the evolution of post-mating courtship. The Fringillidæ are, on the whole, somewhat similar to the Sylviidæ, save that the colour-dimorphism is usually more marked and the male usually incubates less. E. Howard ('20) has recently shown that territory plays a great part in the lives of birds, and that, in both Sylviidæ and Fringillidæ, it is the male who, early in the season, before other manifestations of sexual emotion, occupies a definite territory. Singing then begins, and is associated with the possession of territory. The process of mating-up consists mainly in the disputes of females for occupied territories with their contained males (Pl. 15. fig. 7). Since the whole breeding-life of the birds is connected with the staking-out of territory at the earliest possible opportunity by the males, it follows that

these must possess different instincts from the females—instincts which begin to react to seasonal influences some time before any reaction occurs in the other sex. Here we have a primary basis for the rest of the dimorphism observed—a basis given by territory requirements, not by epigamic needs.

In birds with both sexes similar in appearance and with mutual courtship, two salient facts are to be noted. In the first place, the birds are usually not protectively coloured, or at least not to such an extent as in most dimorphic species. Take for example the Herons and Egrets, the Swans, the Gulls, and many of the cliff-dwelling and other sea-birds (Guillemots, Razorbills, Petrels, &c.). The Grebes and Divers are intermediate—the main coloration is protective, but the head, neck, and under-surface are conspicuous and used in courtship. In the second place, both sexes almost always share in nest-building, and often in incubation and the care of the young. So far as I know, there are no birds with mutual courtship in which the males do not share some of the duties of parenthood, and their share is on the average certainly greater than is that of the males of birds with dimorphism in courtship. Also the nest-site is, usually at least, chosen by both birds jointly.

It appears to be definitely the case that several tendencies are at work to produce the variation in modes of courtship that we see. (1) Where, as in the Warblers, &c., the whole life-cycle is based on the early staking-out of territory by the males, there must be a dimorphism of instinct in connection with this, and this primary dimorphism tends to be continued in other ways, *e. g.* courtship. (2) Where protective coloration is of great importance to a species, it is imperative that one sex at least shall be thus protected; this sex will naturally, save in very exceptional cases, tend to be the female. If protective coloration is desirable, it will almost always follow that general inconspicuousness will be desirable; this will mean that any violent manifestations of emotion, whether in the form of song or of display, will be undesirable. Hence there will be a tendency in such species to depress the level of sexual excitability in the females. This in its turn will, however, make it necessary for there to exist some mechanism for arousing their sexual emotion, and this will naturally be found in the courtship of the male. Thus in general the necessity for inconspicuousness in the female will have as natural reaction a tendency for courtship activities to be confined to the male, and to be well developed in him. Inconspicuous females tend to be associated with dimorphism of courtship, and often of colour. The tendencies mentioned in (1) and (2) often interact so that it is hard to distinguish which is the primary. Where polygamy prevails, and the males take no share in parental duties, this tendency will naturally produce its most marked results. (3) In some groups, such as for instance the Herons, not only is it necessary for both birds to share in feeding the young, but also to share the duties of incubation (since the feeding-

grounds are so distant; furthermore, protective coloration, as in most colony-breeding birds, is unnecessary. Here we find two tendencies acting in the direction of similarity in appearance and behaviour. In the first place, there is no need for the female to be inconspicuous, whether in plumage, voice, or action; thus, *ceteris paribus*, there will be no tendency to restrict any variations in the direction of greater conspicuousness—even if they may have been first acquired by the male sex, which is by no means necessary—to the males. Secondly, since the male as well as the female must possess the instinct to incubate and to feed the young, it follows that there is a tendency to approximate the instincts of the two sexes in these particulars; and the sex-similarity thus initiated again tends to be continued in other ways, unless there are reasons to the contrary, which, in birds to whom inconspicuousness is a matter of indifference, we have just seen do not exist. In birds of this type, therefore, there exist again two mutually reinforcing tendencies which tend to bring about a similarity of plumage and instincts, and so lead to mutual courtship.

There are, it is true, species like certain Penguins (Levick, '14) in which the sexes are alike, but much of the courtship is not mutual; there are other species, like our Red-throated Diver, in which the sexes are similar and there exists mutual courtship, but in which the male helps to a comparatively small extent in incubation. In such a complicated subject we should not expect to find universal hard-and-fast rules; each case requires to be investigated on its merits, and with a thoroughness which has so far only characterised few workers. But that the two general tendencies which I have mentioned, to dimorphism and to mutualism, do exist, and that they are definitely correlated with other characteristics of the species' life-history in the general way I have sketched, appears to be incontestable.

One other point remains to be considered here. Why is it that among birds with mutual courtship, some, like Divers and Grebes, perform ceremonies far from the nest, no emotional expression being seen at or close to the nest during incubation and the care of the young, whereas in others, such as Herons, Egrets, Pelicans, &c., the chief ceremonies observed are those which take place at the nest or nest-site, especially at the moment when one bird relieves the other from the duty of incubation? (Pl. 14. figs. 5 & 6).

The answer is not, I think, far to seek. The "nest-relief birds," as we may call the latter category, are all species in which the nest is not concealed, and does not appear to be in need of special protection against enemies. In most cases the birds nest in colonies. The birds with mutual ceremonies which are unconnected with nest-relief, on the other hand, have nests which are carefully concealed, or at least are far from conspicuous, and rarely breed in colonies.

When a sitting bird is rejoined by its mate, especially if the mate's presence implies a speedy relief from the tedious business of incubation,

it is natural that emotion should be aroused. If there is no biological reason against the expression of the emotion, it will naturally be expressed then and there in some form of ceremony. On the other hand, if there are biological reasons for concealing the position of the nest from enemies, then it will be desirable not to draw attention to the spot by conspicuous sounds and actions, and selection will see to it that the emotion is not expressed immediately and naturally at the nest, but at a distance from it. The fact that, in the Crested Grebe, there exists a special and very elaborate ceremony which occurs when the members of the pair rejoin each other after having been separated for some time, indicates that in this species too the same emotions occur in similar circumstances, but are not allowed expression in the neighbourhood of the nest.

Here again, therefore, we find an influence of the general mode of life upon the form of the courtship. So that we may really say that, although, given in the first place the state of general excitement produced by the sexual hormones, in the second place the stimulative effect of sexual display, and thirdly the necessity for regulating coition, there will inevitably come into being displays, &c., which go by the general name of courtship, yet the *form* of the courtship, not merely in details but in broad lines as well, will depend in the main upon other general biological factors affecting the species.

There remains to be considered the physiological and genetic mechanism which we must suppose responsible for the phenomena; but before passing to this, I should like to summarize briefly the conclusions just reached. In few words they are these:—

1. Polygamy encourages sexual dimorphism. It is only found among birds with nidifugous young, since nidicolous young require that both parents should assist in feeding.
2. Need for inconspicuousness encourages dimorphism.
3. Nidifugous habit in the young facilitates the development of dimorphism otherwise initiated.
4. Early occupation of territory by one sex encourages dimorphism.
5. Absence of need for inconspicuousness encourages mutualism.
6. Need for incubation by both parents encourages mutualism.

In addition, there are no doubt many special physiological points which encourage one or the other tendency; but in general the condition observed is the result of the interaction of the tendencies we have enumerated.

Recent experimental work is beginning to give us an insight, albeit but a partial one as yet, into the physiological and genetical mechanism underlying sex-characters in birds.

It appears that castration of a male, in highly dimorphic species like fowl and wild duck, produces birds which are neutral in instincts but remain male in plumage.

In females, on the other hand, castration produces cock-feathering, but not male instincts.

Recently investigations have been made on breeds of fowls like the Sebright Bantams, in which the cock is hen-feathered. Two interesting points have emerged. The first is that the condition is due genetically to a Mendelian gene, the second that it is due physiologically to the fact that the male gonad in these animals possesses the same substance as do the gonads of normal females, which inhibits the development of male plumage. This latter point is demonstrated by castrating hen-feathered cocks, upon which they become cock-feathered—a strange but conclusive result (Morgan, '19). Morgan believes that the condition has its histological basis in the development of luteal cells in the testes of hen-feathered cocks, similar to those found in the ovaries of normal hens, but recently Pease ('19; *q. v.* for references to previous work) has thrown doubt on this.

In any case, the facts are of great interest as showing by how simple a means, and in how few generations, a dimorphism of plumage could be converted into a similarity. On the other hand, it also shows that in this dimorphic species at least, plumage and instincts (as the castration experiments also demonstrate) depend upon different mechanisms for their development. The development of male or female instincts is due to a positive effect exerted by some secretion of the male or female gonads respectively, acting upon a basis which is neutral in the absence of the specific secretion, whereas the male gonad has no positive effect upon plumage development (the plumage of capons being, if anything, more male than normal), while the female gonad exerts in this respect an entirely inhibitory effect.

It must be emphasized, however, that we have no experimental information with regard to species with similar plumage and courtship (in passing, it may be remarked that the castration of Grebes or Herons should provide interesting results). Further, from the general considerations advanced above, it is clear that we should not expect precisely the same mechanism to hold good in "mutual" as in dimorphic species. In the latter, as we have seen, selection must have been at work emphasizing and exaggerating any sexual differences of instinct which primitively existed; whereas in the former all the influence would tend in the other direction, of assimilating instinct in the two sexes.

To what pitch this has as a matter of fact been carried is shown by the observations of Selous and myself upon the Crested and the Little Grebe (Dabchick). The Grebes are birds in which mutual courtship attains the highest development yet described, and in which sexual adornments similar in the two sexes attain a great specialization. In the two species mentioned, and probably in others, the instincts of the sexes are so alike that coition occurs both in the normal or in the reversed position. In these birds, coition always takes place upon a nest; the "passive" bird extends itself at full length in a perfectly horizontal position, the "active" bird mounts the other from behind, and, after coition, walks up its body and off by its shoulder.

The differentiation of action between the sexes is thus very considerable ; yet in spite of this, as I say, either sex adopts either position according to circumstances. In the Moorhen, Selous ('02) has described reversed pairing as a normal sequence of pairing in the usual position. Mr. E. Howard tells me that he has repeatedly had occasion to confirm this himself. In Doves and Pigeons it may also occur (Whitman & Riddle, '19 ; Marshall, '22, p. 690).

It should be remembered that sexual dimorphism to any marked extent is a late development in most groups. Primary and accessory organs are, naturally, different, but general coloration and body-form is usually similar in both sexes in primitive animals—*e. g.* Echinoderms, many primitive insects ; Crustacea and other Arthropoda, Cyclostomes and most fish. In any case, recent work has made it abundantly clear that the genes for the secondary sexual characters of both sexes are normally carried in all members of the species, and that either the sex-chromosome mechanism ensures two quite different types of cellular metabolism, one permitting the development of male, the other of female characters, as seems to be the case in insects, or else that special hormones are developed in the gonads which exert specific growth-promoting effects upon some sexual characters, inhibiting effects upon others, as in vertebrates (summaries in Marshall, '22, ch. 15 ; Goldschmidt, '20 ; Huxley, '22 a).

If, therefore, the divergence which I have referred to between the sexually dimorphic and mutualist types of birds originated early, as it seems to have done (for the distinction characterizes whole groups of the class), we may suppose that the primitive bird species on which it acted were probably similar in appearance, without well-marked courtship colours or structures, whether in one or in both sexes, and with a moderate dimorphism of instincts. Later development has either accentuated the difference of instincts, as in the Sylviidæ, or the divergence of instincts and of appearance, as in most Gallinaceous birds ; or has allowed bright colours to develop, apparently for use in courtship, but has not confined them to one sex, although it has not closely approximated the instincts of the two sexes (as in the Penguins, Levick, *loc. cit.*), or finally has encouraged sexual adornments similar in the two sexes, together with markedly mutual courtship, and has approximated instincts to a high degree—as in the Grebes.

So far as observation can be a guide in these matters, it appears that although sex-dimorphism in plumage may depend upon different genetic and physiological factors from that in instincts and from that in size, yet as a matter of evolutionary fact, the first two, and probably the third also, have gone hand in hand.

In other words, the divergence between dimorphic and mutualist species is primarily dependent on whether the gonadial hormones remain as similar as is compatible with primary sex-differentiation, or whether they become considerably different in the two sexes. If they adopt this latter alternative,

then there will result, unless special circumstances arise, a simultaneous dimorphism in both appearance and instincts; if they remain on the whole similar, there will be (again unless there are special reasons against it) a similarity between the sexes, not only as regards appearance, but also as regards courtship and parental behaviour.

If this turns out to be well founded, and the gonads do normally in birds determine appearance, behaviour, and size simultaneously, then it is clear that observation will have contributed important guiding lines for future genetic and evolutionary research.

In conclusion, I would like to emphasize the fact that, even when both sexes are similar, there is often no doubt whatever that the coloration and special structures used by them both in courtship have been evolved in relation to sexual habits, and in essentially the same way as bright colours and special structures used in courtship by males alone in dimorphic species. They have arisen through the necessity of providing an emotional stimulus to the other member of the pair, if fertilization is to be normally and easily effected, particularly in the face of adverse environmental conditions; and from the reverse point of view, have become necessary because it is biologically desirable to keep the mean sexual excitability of the pair at a level low enough to prevent excessive coition. They are, to use the useful term of Poulton's which I have for some time adopted, always *epigamic*, although not always *secondary sexual* characters. They have also been usually grafted on to primitive ceremonies which are the direct outcome of sexual excitement, and indirectly often the result of an "engagement" period which is caused by non-sexual exigencies of the life-cycle.

Although the direct competition among males, which was one of the main points of Darwin's theory of sexual selection, does not appear to occur in the evolution of most epigamic characters among birds, yet it is noteworthy that in the polygamous species in which it *does* occur, the type of coloration and structure which is evolved is very similar to that evolved in monogamous species, except that development has usually gone to further lengths of specialization. This similarity between the end-results in what we may call "accessory" as well as in "sexually-selected" epigamic characters, is due to the second salient fact first clearly recognized by Darwin—the fact that the development of an epigamic character is dependent upon the emotional effect which it produces upon the mind of a bird of opposite sex. Epigamic characters must be emotionally stimulative if they are to perform their function successfully; and to be emotionally stimulative, it would appear that they must be first striking, and secondly not usually visible, so as to have, when they are displayed, an element of novelty and unfamiliarity which adds to their stimulative effect. So far as their striking quality is concerned, they may be either what seems to us beautiful or else what seems to us bizarre. So far as unfamiliarity goes, it should be remembered that many epigamic

characters are special structures only fully displayed during courtship (*e. g.* scapulars of Egrets, tail-coverts of Peacock, ruff of Crested Grebe); others are special patches of colour only made prominent by special display actions (*e. g.*, white on wings of Blackcock and of Crested Grebe, red of legs of Redshank, rich purplish-brown of neck of Louisiana Heron); while still others, although always present, are probably not prominent unless the two birds are close to each other, and in certain relative positions characteristic of courtship. This is probably the case with many of the curious patterns characterizing the *front view* of birds at short range (*e. g.* Blue Tit, Turnstone, Redstart, Ringed Plover); that this is the probable explanation is shown by the fact that when special structures with undoubted epigamic function are developed on the head, these are often displayed so as to appear most striking (or only so) when seen in this way, close up and from the front (*e. g.* the ruff and ear-tufts of the Crested Grebe, the crest of Louisiana Heron and Little Egret).

The existence of true sexual selection as found in polygamous species thus encourages the same tendencies in epigamic characters as does the selection of those with a purely "accessory" function; but, owing to the fact that in polygamous species the males take no share in incubation or the care of the young, dimorphism can proceed to its limit, and owing to the fact that there is a real selection as between different males, and so greater competition in regard to secondary sexual characters, and that the successful male transmits his qualities to a greater number of offspring, the process of evolution of epigamic characters is not only more rapid, but also is generally carried to a higher pitch than in monogamous species. In other words, polygamy and its attendant true sexual selection simply accentuate the same processes that are operative whenever epigamic characters are being evolved, even in the absence of sexual selection proper.

This development of epigamic characters in relation to the *mind* of the opposite sex is a point of very general biological interest, since it is the only example, in organisms below man, of a secondary effect of the mind of a species upon the evolution of that species. Mental qualities of course normally have survival value, but this is quite a different matter; they thus determine the survival or extinction of the species, not its modification in new ways. The mind of one species may play a part in moulding the evolutionary development of *other* species, as when acute vision on the part of predaceous animals renders concealing coloration advantageous, or the visual and olfactory preferences of flower-visiting insects are reflected in the development of colour and scent in the flowers visited. Lloyd Morgan ('21) has recently emphasized the influence of mind upon evolution by introducing the useful term "Psychical Selection." As indicated above, however, further terms are needed to distinguish between psychical selection acting upon the evolution of *other* species, as in the case of the mental qualities of bees influencing the evolution of flowers, or upon the evolution of the *same* species, as in the development

of stimulative display characters. If the barbarism be permitted, the terms "heterospecific" and "autospecific" psychical selection might be employed to make this distinction. But once epigamic characters come to be advantageous, the mind of the species (in the females in sexually dimorphic forms, in all individuals in those with mutual courtship) is exerting the indirect effect we have been describing upon the future development of colour, structure, and behaviour in the race. This is the most important fact which Darwin perceived, and this stands firmer than ever in spite of the rejection of the bulk of the other part of his doctrine.

In concluding, I should like to thank Professor Lloyd Morgan, Mr. Eliot Howard, and Mr. A. M. Carr-Saunders, all of whom have kindly read the foregoing article in manuscript, and have helped me with several important criticisms and suggestions.

New College, Oxford,
March, 1923.

POSTSCRIPT 1.—Since the above was written, Dr. J. C. Mottram has been good enough to write to me on a number of points concerning sexual coloration in birds, and to allow me to see the MS. of an unpublished paper on the subject. I would like to take the opportunity of dealing with a few of the points which he raises in this and in his book ('14).

He points out the great importance in many birds of concealing coloration—a proposition in which every naturalist who has studied birds in the field would agree with him. I have in the body of the paper dealt with the ways in which the necessity for concealment or its absence reacts upon the "courtship" characters and activities of birds.

With reference to the Kingfisher (*Alcedo ispida*), Dr. Mottram makes out a strong case for believing that its brilliant colouring, present of course in both sexes, is aposematic, with the function of warning possible enemies of the bird's unpalatability. He points out that records of the Kingfisher being attacked by birds of prey are extremely rare; and has found that its flesh is unpalatable to man and rejected by domestic animals.

However, if the Kingfisher really, as seems probable, presented an example of warning coloration, it would in no way invalidate my general conclusions; it would merely corroborate from a new angle what I have been urging in this paper—viz., that each species of bird must be worked out on its merits, and that coloration and behaviour are always determined not by one single cause, but by several, of which the two most important are (*a*) the bird's relations with its mate, and (*b*) its relations with its enemies and its prey.

Dr. Mottram, however, goes farther. He attempts to account for *all* "courtship" characters and actions solely in terms of the bird's relations with enemies and prey.

(1) By an ingenious train of reasoning he points out that where the hen alone, or chiefly, incubates, she must be regarded as biologically the more

valuable of the pair, and that in such species the display and song of the cock has as its primary function that of drawing the attention of enemies away from the hen ; so that, if one of the two is sacrificed, it shall generally be the less "valuable" male.

(2) Where the species is capable of defence, or is unpalatable—*i. e.* does not require protective coloration—he postulates that courtship should be not elaborate, or may even be absent.

(3) Where both sexes are of equal biological value (*i. e.* where both incubate), he postulates that both should indulge equally in display.

The reasoning is undoubtedly ingenious, but can be shown not to be adequate to account for all the facts.

As regards (1), it should be remembered that the song of male "territory birds" is most powerful before any females have arrived. It could be no possible advantage to the species to have attention attracted to the males when there were no females present from whom attention could be drawn off.

It is undoubtedly true that where only the female incubates, and where protection is desirable, dimorphism of sexual characters and behaviour will be encouraged. This I have pointed out in the body of the paper. Dr. Mottram simply restates the problem from a different angle, and with the epigamic side of the matter left out.

(2) is simply not true in a number of cases. Herons and Egrets are well protected from enemies, but have an elaborate courtship. So do Swans (Selous, '13, and my own observations). So do Hawks, though here the displays are concerned with flight, not with bright coloration (Owen, '16-'22, Sparrow-Hawk ; Kestrel, my own observations) ; and other examples could be quoted.

(3) Where both sexes are of equal value, it would appear on the face of it biologically desirable that both should be rendered *inconspicuous* when concealment is in any way desirable, if, as Dr. Mottram would have us believe, the chief function of display is to attract the attention of enemies. However, in the Grebes, all of which take great pains to conceal their nest, and are protectively coloured so long as they are in the normal swimming, feeding, or resting attitudes, elaborate mutual courtship does occur, and at once makes the pair conspicuous. The same, to a less extent, is seen in Divers. The vocal duets of Owls which go on in the breeding-season (Huxley '19) are difficult to account for on any theory which relates them only with attracting the attention of enemies.

Finally, Dr. Mottram makes the point that since many birds "get on" without bright colouring in one or both sexes, and yet reproduce, therefore when bright colouring is present it cannot be supposed to have any relation to reproduction. This, however, is an old fallacy, repeatedly exposed since the early days of the evolution controversy. It would be equally justifiable to say

that because an earthworm gets on without eyes, and yet reacts to light and darkness, therefore when eyes are found, they can have no relation to light-perception; or that because lower mammals get on with a small brain; therefore the difference in brain-size between them and man can have no relation to the functions carried out by the brain of lower mammals; and so on, *ad lib.*

It becomes increasingly clear that to interpret the behaviour and evolution of a bird, even if apparently in only one regard, it is necessary to take into account *all* the circumstances of its life. As regards coloration and "courtship" behaviour, I hope I have shown that relation to enemies and relation to the mate are two factors of greatest importance. I am grateful to Dr. Mottram for having brought to my notice a number of points concerning the relation of birds to their enemies of which I was not aware; and I believe that his contribution to the theory of the subject is of real value. But so long as cases remain—as they do in large numbers—where coloration, structure, or behaviour have an obvious function in regard to the opposite sex, and no discoverable function in relation to the enemies or any other factor of the bird's life, I maintain that we must take these into account, and that Dr. Mottram is definitely wrong in attempting to base his theory of the evolution of courtship solely on one, instead of on both of the two main factors mentioned above.

On the other hand, his suggestion that the bright colour and general conspicuousness of the male may have in some species the function of drawing the attention of enemies from the biologically more valuable female will, I believe, prove of importance in certain puzzling cases. I will mention but two. In the first place we have the well-known fact that many mimetic species of butterflies, including some of the most striking examples of mimicry (e. g. *Papilio dardanus*), are mimetic in the female sex alone, the male being conspicuous but non-mimetic. The males are "valuable" only before copulation: the females until after oviposition, and further, have usually a poorer flight. If a certain average toll is taken of the species by enemies, it could well be a real advantage to have it fall preponderatingly on the male sex.

The second example concerns birds. Reflection will show that the bright colours of male birds fall broadly into two categories—those which, like the "tail" of the Peacock or Argus Pheasant, are only conspicuous in display, and those which, like the general coloration of most male ducks, are always conspicuous. It will be further found that the former are definitely *displayed*, the latter usually not. *E. g.*, the display of male ducks is largely a bobbing of the neck; the general bright body-colour is not made more conspicuous in display. The male duck, furthermore, (i.) takes no share in incubation or rearing the young, (ii.) usually stays near the hen until the young are hatched, (iii.) as soon as he leaves the hen, moults into eclipse (protective) plumage. (iv.) The hen is protectively coloured. (v.) The species is highly palatable and much attacked by Raptores.

Thus there is a good *prima facie* case for applying Dr. Mottram's ideas to cases of bright coloration in the males of palatable species in which the bright colour is not specially associated with display, and especially in forms in which the female alone looks after eggs and young.

It is, however, becoming clear that many side issues of the problem can best be attacked by statistical methods: and this I propose to do as opportunity offers.

POSTSCRIPT 2.—The last number of 'British Birds' (vol. xvi. p. 318) contains an article by Mr. N. Gilroy on the nesting habits of the Black-throated and Red-throated Divers to which reference should be made.

The Black-throated Diver is mentioned as dipping its bill in the water when nervous because scared off its eggs. This extends my observations of the beak-dipping of the Red-throated Diver to another species.

Of courtship, the following remark is made—"The pairs may be observed on the tarns for a considerable time before nesting begins, and one is frequently treated to the extraordinary display which takes place, not only during courtship and pairing, but even when actual breeding has commenced—when both birds propel themselves through the water almost vertically." This, so far as it goes, confirms my observations.

J. S. H.

8th May, 1923.

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EXPLANATION OF THE PLATES.

PLATE 14.

- Fig. 5. Louisiana Heron (*Hydranassa tricolor*). Twig-bringing ceremony after nest-relief. The relieved bird is presenting a twig to the bird on the nest. Note raising of crest, aigrettes, and neck-feathers, and spreading of wings.
- Fig. 6. Nest-relief ceremony of Little White Egret (*Egretta candidissima*). The bird on the right is about to step off the nest. Note erection of crests and aigrettes, and spreading of wings.

PLATE 15.

- Fig. 7. Two female Whitethroats (*Sylvia cinerea*) fighting for a male and his territory; the male watching.
- Fig. 8. A pair of Willow-Warblers (*Phylloscopus trochilus*); simultaneous performance of wing-flapping ceremony.



FIG. 5.—Louisiana Heron (*Hydranassa tricolor*). Twig-bringing ceremony after nest-relief. The relieved bird is presenting a twig to the bird on the nest. Note raising of crest, aigrettes, and neck-feathers, and spreading of wings. (Photo by J. S. H.)



FIG. 6.—Nest-relief ceremony of Little White Egret (*Egretta candidissima*). The bird on the right is about to step off the nest. Note erection of crests and aigrettes, and spreading of wings. (Photo by J. S. H.)



FIG. 7.—Two female Whitethroats (*Sylvia cinerea*) fighting for a male and his territory; the male watching.
Reproduced by permission from E. Howard, 'The British Warblers.'



FIG. 8.—A pair of Willow-Warblers (*Phylloscopus trochilus*); simultaneous performance of wing-flapping ceremony.
Reproduced by permission from E. Howard, 'The British Warblers.'